Land Snail Fauna of Mé Auré Cave (WMD007), Moindou, New Caledonia: Human Introductions and Faunal Change[1]

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Abstract: The land snail fauna excavated from a cave at Mé Auré on the central southwestern coast of New Caledonia represents a period of over 3000 yr, from before human arrival in the island to the present. The material excavated represents 20 terrestrial species in nine families. The fauna reflects the overall land snail fauna of New Caledonia in being dominated by small snails in the families Charopidae and Rhytididae, with large *Placostylus* species (Bulimulidae) present and minor representation of other families. Two alien species are present: *Allopeas gracile*, probably introduced before European arrival, and *Achatina fulica*, introduced in 1972. There are suggestions of change in the composition of the fauna, perhaps associated with the arrival of Europeans and the replacement of native by alien vegetation, with *Andrefrancia vetula* and possibly *A. saisseti* declining and *Rhytida aulacospira* increasing.

Dating of archaeological material is fundamental to interpreting prehistoric events, and assessment of environmental change, including human-induced change, is a major part of archaeological research. Radiocarbon dating and pollen analysis (e.g., Athens et al. 1992, Athens and Ward 1993, Allen 1994), among a range of methods, are some of the most important tools available to the prehistoric archaeologist. Often, however, analysis of the land snail fauna can be of additional value, providing corroborating evidence or allowing additional inferences regarding both dating and environmental change (Evans 1972, David and Stanisic 1991, Goodfriend et al. 1994). For instance, if the habitat or microhabitat preferences of the species recovered are known, changes in faunal composition through the layers of an archaeological excavation can inform us about environmental change. Land snails can be used as material for radiocarbon dating (e.g., Goodfriend and Mitterer 1993), with the proviso that in limestone areas age anomalies may occur (Goodfriend 1987). And if certain species known to be nonnative human introductions are found only above a particular horizon, then inferences can be drawn regarding the date of arrival of humans in the locality, or if that date is known from other evidence the snails offer corroborating evidence.

In the Pacific, land snails recovered in archaeological excavations have been analyzed from all these perspectives, notably in Hawai‘i (Christensen and Kirch 1986, Dixon et al. 1997), the Solomon Islands (Christensen and Kirch 1981), American Samoa (Kirch 1993), the Pitcairn Islands (Preece 1998), and the Cook Islands (Allen 1992). Despite possible problems associated with taphonomic processes, especially mixing of soil layers resulting from various disturbance factors (Carter 1990, David and Stanisic 1991, Goodfriend and Mitterer 1993), important inferences have been made. In particular, because certain nonnative species are known to have been introduced widely by prehistoric people as they colonized the islands of the Pacific, and because others have only been introduced since Western discovery of the islands, the composition of the snail faunas has been used to corroborate the timing of prehistoric

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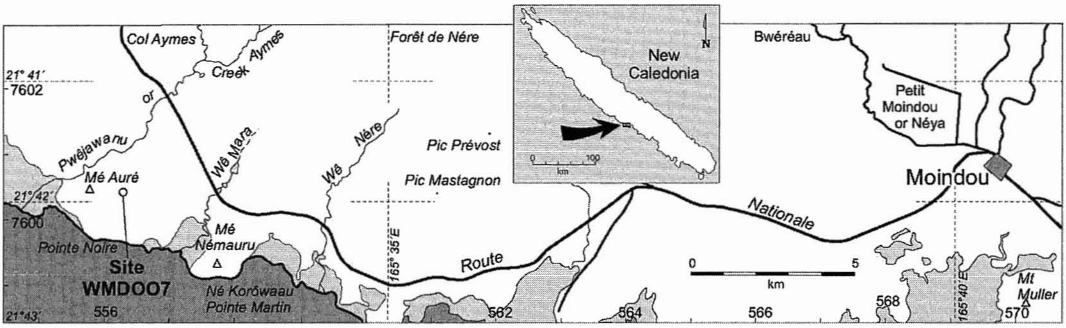

FIGURE 1. Map showing the location of Mé Auré cave, archaeological site WMD007.

human colonization and the dating of particular archaeological horizons. Nevertheless, although a useful method, land snail analysis remains relatively little used in the Pacific (with the above notable exceptions), and no such analysis has been reported from New Caledonian deposits.

The land snail faunas of cave deposits have attracted particular interest (Evans 1972, David and Stanisic 1991, Goodfriend and Mitterer 1993) because they are often well preserved, having been protected from exposure. In this study we analyzed the land snail fauna of a cave deposit in New Caledonia to investigate environmental change over time and human colonization of the region.

MATERIALS AND METHODS

Location, Excavation, Sampling, Dating

Figure 1 shows the location of the cave (designated WMD007 in the catalog of the Département Archéologie, Service des Musées et du Patrimoine de Nouvelle-Calédonie) on the central southwestern coast of New Caledonia. It lies ca. 13 km west of Moindou, 500 m east of Mé Auré, and 750 m north of the coast at grid reference 5563.6004 on Sheet SF-58-X-4a (no. 4824, Moindou) of the 1:50,000 Série Orange, Institut Géographique National de France (1991). The cave is situated on the northeastern flank of a low hill ca. 30 m below the summit and 50 m above high-tide mark in mixed broadleaf forest. More details are given by Grant-Mackie et al. (2004).

For excavation, the floor was divided into an irregular grid (Figure 2). Only areas 1 and 3 were investigated for snails. The top 5 cm of unconsolidated material was cleared from each area and removed for sorting. Plant debris, limestone fragments, and material cemented by modern bird feces were discarded. The underlying areas were excavated by trowel and material was removed for laboratory analysis. More details of the excavation methods are given by Grant-Mackie et al. (2004). Area 3 was mostly sampled at regular depth intervals of 10 cm, but this was not possible in area 1 because of the irregular scatter of larger limestone clasts through the sequence. This also meant that the volume of spoil processed for snails varied considerably among collections. The following are indicative: for NC/f1246 (Figure 3), ca. 0.025 m^3; for NC/f1247, ca. 0.05 m^3; for NC/f1248, ca. 0.125 m^3; and for NC/f1249, ca. 0.15 m^3 (for explanation of sample numbers, see under next subheading). Snails were sorted from other material by handpicking under a low-power microscope or mounted lens or, for larger fractions, with the naked eye. Despite the fact that the <3-mm fraction was checked for material before being discarded, and no notable organic remains seen, it is likely that some juvenile and very small adult shells were overlooked and thus not included in the analysis.

Two samples were submitted to the Uni-

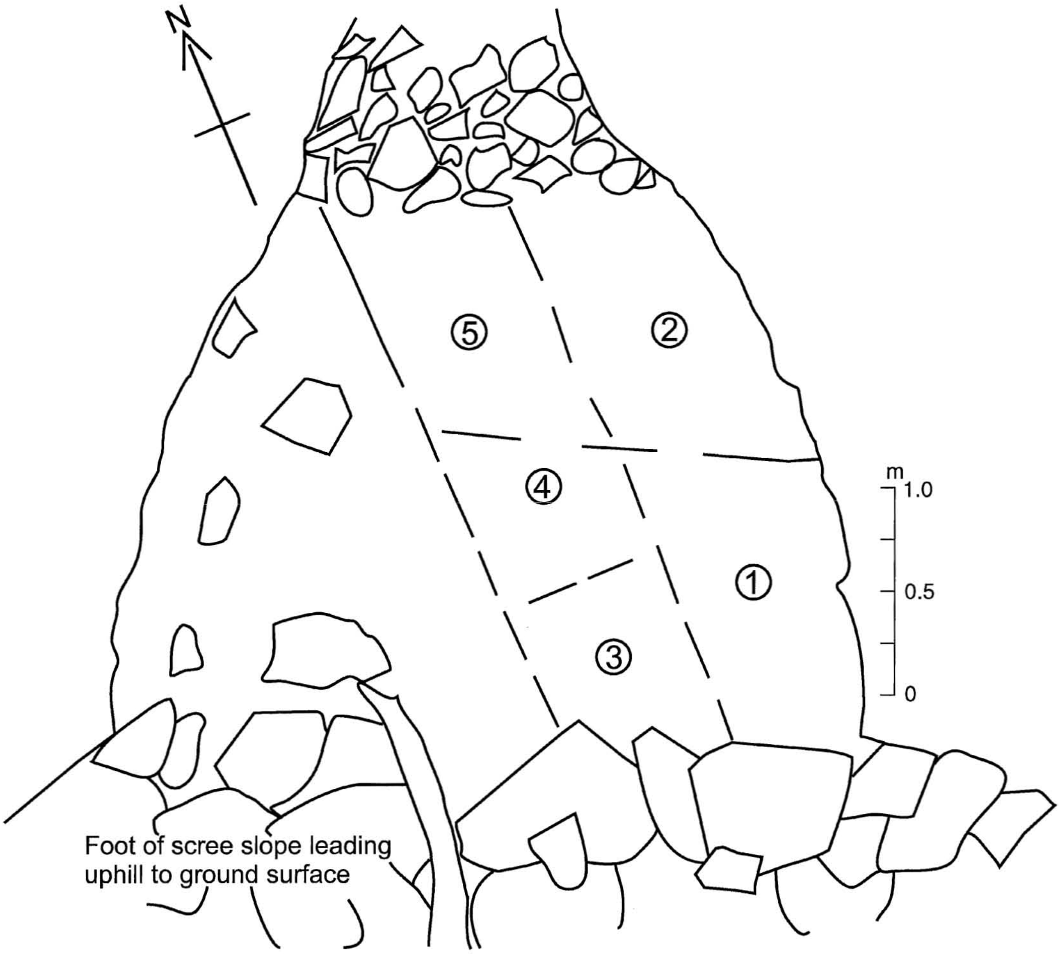

FIGURE 2. Plan of cave floor, with entrance at the bottom of the diagram, showing larger fallen blocks of limestone, the grid system used for collection and excavation purposes (straight dashed lines), and the numbered collection areas.

versity of Waikato Radiocarbon Dating Laboratory, New Zealand. One was a land snail shell, *Placostylus duplex* (Gassies 1871), from a depth of 75 cm, the other a sliver of human tibia from a depth of 37 cm, both from area 1.

Snail Identification, Preservation, Faunal Trends

Snail species were identified by reference to the literature and in some cases by comparison with previously identified specimens in the Bishop Museum (Honolulu). The literature used included the monograph of Franc (1957), the checklist of Solem (1961), and various other publications (Pilsbry 1906–1907, Solem 1959, Mordan and Tillier 1986, Tillier and Mordan 1995).

Because of the poor knowledge of the fauna, identification of the collected material was difficult in some cases. A number of clearly recognizable species could not be readily referred to named species (they may be undescribed) and are hence referred to "*Pleuropoma* sp.," "*Pararhytida* sp.," "?*Microcystis* sp.," and "*Rhytida* cf. *aulacospira*."

All material is deposited in the collections of the Department of Geology, University of Auckland, under both AU (Auckland Uni-

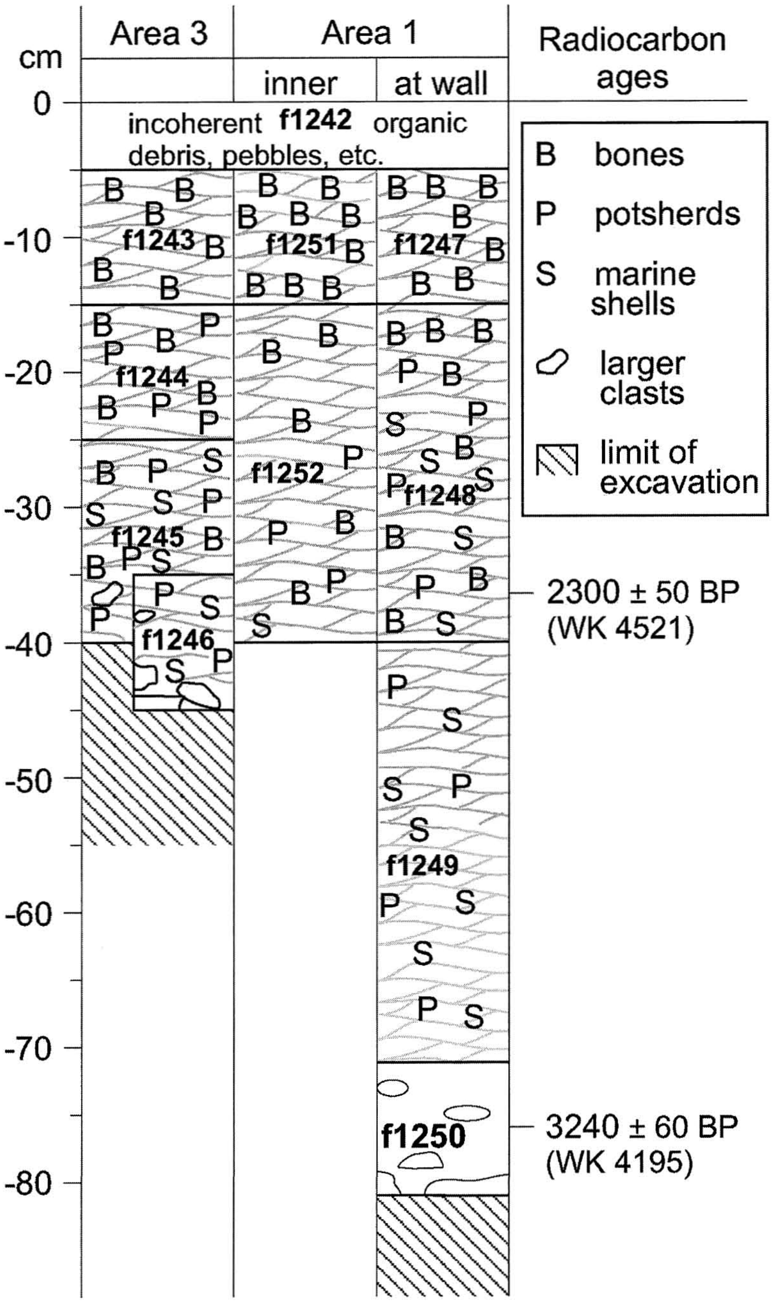

FIGURE 3. Stratigraphic columns for areas 1 and 3 showing the collection sites (f1242, etc., which should be prefixed by NC/ to give the full reference number), the distribution of various materials, and the horizons of two radiocarbon dates (BP, years before present; WK . . . , sample number in the University of Waikato Radiocarbon Laboratory records). The lozengelike background pattern over much of the diagram denotes finely interbedded lenses of gray ash and charcoal, reddish soil, and shell and/or bone debris; the deepest part of area 1 (NC/f1250) consisted of structureless reddish spoil with rock clasts and *Placostylus* shells; the top 5 cm of the cave floor likewise showed no discernible bedding.

versity) and NC/f (New Zealand national catalog of New Caledonian fossil localities) catalog numbers. Only the NC/f numbers are referred to herein.

Changes in relative abundance of individual species with stratigraphic depth were analyzed statistically using log likelihood *G* tests (Sokal and Rohlf 1981).

RESULTS

Stratigraphy, Dating

Figure 3 shows the stratigraphy for areas 1 and 3, with the snail sample numbers indicated. The human bone, from a depth of 37 cm, was dated (uncalibrated) at 2,300 ± 50 yr B.P., with a δ13C value of −13.6 ± 0.2‰. The *Placostylus duplex* shell that was used for radiocarbon dating, from a depth of 75 cm, returned an uncalibrated age of 3,240 ± 60 yr B.P., with a δ13C value of −9.97 ± 0.2‰. These conventional dates may not be very accurate for a number of reasons, including possible uptake of old carbonate from limestone substrates by snails (Goodfriend 1987), an unknown marine contribution to the vertebrate diet, contaminants remaining in the samples as a result of the limited pretreatment process, and limited isotopic data; for a fuller discussion see Grant-Mackie et al. (2004). Nevertheless, the dates accord with the stratigraphy and human history of the cave (Grant-Mackie et al. 2004). Depths below 70 cm predate human colonization of the area (ca. 3,000–3,500 yr ago for New Caledonia as a whole: Frimigacci 1980, Morat 1993, Gargominy et al. 1996); the 20-cm depth represents the end of the Lapita cultural period (cessation of pottery production), estimated as about 1,700 yr B.P. (Kirch 1985); and the 15-cm depth represents the arrival of Europeans, in 1774 (Gargominy et al. 1996). Despite the problems mentioned here we therefore accept these dates as approximately correct.

Postdepositional Disturbance

On the basis of its appearance during excavation the sequence seen was essentially undisturbed by postdepositional processes. The matrix was almost entirely dry, very fine wood ash and small charcoal fragments in thin (up to 20 mm) lenses of dark and light gray and reddish brown color, and including charred or burnt bone and shell. Interfingering with these were structureless concentrations of small bones (rodent, bird, lizard, frog, bat, and fish), crab claws, marine mollusks, pottery shards, and human bone fragments. Land snails were present throughout. Bedding contacts were mostly sharp and clearly distinct as a result of color contrasts, with no indication of digging, burrowing, or other disturbance. The only intrusions were root penetration. The top 5 cm of the cave floor was incoherent and showed no discernable bedding.

Snail Taxa Recovered

The species recorded in each sample are listed in Table 1. In total, 225 intact nonmarine snail shell specimens were collected. In addition, about 20 shells of *Achatina fulica* were recorded but not collected, and numerous fragments of *Placostylus* sp(p). shells were collected. These records represent 20 terrestrial species in nine families, and one freshwater species (probably a contaminant [see under Family Planorbidae]). The fauna reflects the overall land snail fauna of New Caledonia in being dominated by small snails in the families Charopidae and Rhytididae, with large *Placostylus* species present and minor representation of other families. Two species are known human introductions. The following paragraphs provide brief information about the species recovered, treating the families in the taxonomic sequence of Solem (1961).

FAMILY HELICINIDAE. Pacific island helicinids are poorly understood taxonomically. Franc's (1957) treatment followed Wagner (1905, 1907–1911), but Solem (1961) considered Wagner's works to be full of errors and, pending further study, placed all the New Caledonian helicinids in *Pleuropoma*, which we follow here. Our material includes a large species, tentatively identified as *Pleuropoma primeana*, and a smaller species that we refer to as *Pleuropoma* sp. The former was found in

TABLE 1

Land Snail Species and Number of Specimens Recorded, by Sample and Depth, with Their Status as Native or Introduced to New Caledonia

Sample	Depth (cm)	Family	Species	No. of Specimens	Native/ Introduced
NC/f1242	0–5	Subulinidae	*Allopeas gracile* (Hutton, 1834)	2	Introduced
		Achatinidae	*Achatina fulica* (Bowdich, 1822)	~20	Introduced
		Charopidae	*Andrefrancia dispersa* (Gassies, 1863)	1	Native
		Charopidae	*Andrefrancia vetula* (Gassies, 1858)	1	Native
		Helicarionidae	?*Microcystis* sp.	6	? Native
		Rhytididae	*Rhytida* (*Pythorhytida*) *aulacospira* (Pfeiffer, 1846)	18	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) cf. *aulacospira* (Pfeiffer, 1846)	5	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) *inaequalis* (Pfeiffer, 1854)	5	Native
NC/f1243	5–15	Helicinidae	*Pleuropoma* sp.	1	Native
		Subulinidae	*Allopeas gracile* (Hutton, 1834)	1	Introduced
		Charopidae	*Andrefrancia vetula* (Gassies, 1858)	12	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) cf. *aulacospira* (Pfeiffer, 1846)	1	Native
NC/f1251	5–15	Charopidae	*Andrefrancia vetula* (Gassies, 1858)	7	Native
NC/f1247	5–15	Helicinidae	*Pleuropoma* sp.	1	Native
		Charopidae	*Andrefrancia dispersa* (Gassies, 1863)	4	Native
		Charopidae	*Andrefrancia taslei* (Crosse, 1874)	3	Native
		Charopidae	*Andrefrancia vetula* (Gassies, 1858)	4	Native
		Helicarionidae	?*Microcystis* sp.	6	? Native
		Bulimulidae	*Placostylus* (*Placostylus*) *porphyrostomus* (Pfeiffer, 1851)	1	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) *aulacospira* (Pfeiffer, 1846)	24	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) cf. *aulacospira* (Pfeiffer, 1846)	11	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) *inaequalis* (Pfeiffer, 1854)	7	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) *gassiesiana* (Preston, 1907)	1	Native
NC/f1244	15–25	Planorbidae	*Physastra sarasini* (Dautzenberg, 1923)	1	Native
		Charopidae	*Andrefrancia vetula* (Gassies, 1858)	6	Native
		Helicarionidae	?*Microcystis* sp.	1	? Native
		Bulimulidae	*Placostylus* sp.	Fragments	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) *inaequalis* (Pfeiffer, 1854)	2	Native
NC/f1252	15–40	Helicinidae	*Pleuropoma* sp.	1	Native
		Helicarionidae	?*Microcystis* sp.	4	? Native
		Bulimulidae	*Placostylus* (*Placostylus*) *porphyrostomus* (Pfeiffer, 1851)	1	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) *inaequalis* (Pfeiffer, 1854)	1	Native
NC/f1248	15–40	Neocyclotidae	*Gassiesa guesterianus* (Gassies, 1866)	1	Native
		Subulinidae	*Allopeas gracile* (Hutton, 1834)	1	Introduced
		Charopidae	*Andrefrancia vetula* (Gassies, 1858)	9	Native
		Charopidae	*Tropidotropis trichocoma* (Crosse, 1868)	1	Native
		Helicarionidae	?*Microcystis* sp.	4	? Native
		Bulimulidae	*Placostylus* (*Placostylus*) *porphyrostomus* (Pfeiffer, 1851)	2	Native
		Rhytididae	*Rhytida* (*Ptychorhytida*) *inaequalis* (Pfeiffer, 1854)	9	Native

TABLE 1 (continued)

Sample	Depth (cm)	Family	Species	No. of Specimens	Native/ Introduced
		Rhytididae	*Rhytida (Ptychorhytida)* cf. *aulacospira* (Pfeiffer, 1846)	1	Native
		Rhytididae	*Rhytida (Ptychorhytida) aulacospira* (Pfeiffer, 1846)	2	Native
NC/f1245	25–40	Charopidae	*Andrefrancia vetula* (Gassies, 1858)	5	Native
		Charopidae	*Pararhytida* sp.	1	Native
		Orthurethra	*Draparnaudia walkeri* (Sykes, 1903)	1	Native
		Bulimulidae	*Placostylus* sp.	Fragments	Native
		Rhytididae	*Rhytida (Ptychorhytida) aulacospira* (Pfeiffer, 1846)	1	Native
NC/f1246	35–45	Bulimulidae	*Placostylus* sp.	Fragments	Native
NC/f1249	40–72	Helicinidae	*Pleuropoma primeana* (Gassies, 1863)	2	Native
		Helicinidae	*Pleuropoma* sp.	1	Native
		Neocyclotidae	*Gassiesa guesterianus* (Gassies, 1866)	6	Native
		Charopidae	*Andrefrancia vetula* (Gassies, 1858)	16	Native
		Charopidae	*Monomphalus bavayi* (Crosse & Marie, 1868)	1	Native
		Charopidae	*Platyrhytida saisseti* (Gassies, 1871)	15	Native
		Helicarionidae	?*Microcystis* sp.	1	? Native
		Rhytididae	*Rhytida (Ptychorhytida) aulacospira* (Pfeiffer, 1846)	2	Native
		Rhytididae	*Rhytida (Ptychorhytida) inaequalis* (Pfeiffer, 1854)	1	Native
NC/f1250	72–81	Bulimulidae	*Placostylus duplex* (Gassies, 1871)	3	Native

sample NC/f1249 (pre-European); the latter in NC/f1243, f1247, f1252, and f1249 (pre- and post-European).

FAMILY NEOCYCLOTIDAE. Franc (1957) and Solem (1961, 1964) used the family name Poteriidae, but this is a junior synonym of Neocyclotidae (Cowie 1998). All New Caledonian species currently are placed in the endemic genus *Gassiesa*. Only seven specimens were found, one in sample NC/f1248 and six in NC/f1249, both pre-European. All were identified as *Gassiesa guesterianus*.

FAMILY PLANORBIDAE. Planorbids are freshwater snails. The species are difficult to distinguish and a number have been widely introduced around the world by people, adding to the confusion. The single specimen found (NC/f1244), however, is identified as the relatively distinct *Physastra sarasini*, a species unique to New Caledonia. We follow Solem (1961) in placing it in *Physastra* rather than Franc (1957), who placed it in *Isidora*. The specimen is small, thin-shelled, shiny, and translucent. It appears recently dead and is probably a contaminant introduced to the cave accidentally, although by unknown means.

FAMILY SUBULINIDAE. A number of subulinid species have been reported from New Caledonia, some described as endemic (Franc 1957, Solem 1961, 1964). These supposed endemics are poorly known and probably can be referred to one of the introduced species (Solem 1961, 1964). Our material is all identified as *Allopeas gracile*. This species is probably of Neotropical origin (Solem 1964) but has been considered "probably the most widely distributed land snail in the world" (Pilsbry 1906–1907:124). It was first reported from New Caledonia in 1859 (Solem 1964), but elsewhere in the Pacific (that is, in the Hawaiian, Samoan, and Solomon Islands [Christensen and Kirch 1981, 1986, Kirch 1993]) it has been shown to be of prehistoric origin. It may be declining in some locations (e.g., the Hawaiian and Samoan Islands), although for unknown reasons (Cowie 2001, 2002, Cowie and Robinson 2003). It was found in samples NC/f1242, f1243 (both post-European), and f1248 (pre-European).

FAMILY ACHATINIDAE. *Achatina fulica*, the giant African snail, was first collected in New Caledonia in 1972 (Tillier 1982, Gargominy et al. 1996). It has been widely introduced throughout the Tropics and subtropics, including to many Pacific islands (Cowie 2002), during the twentieth century. It was found only on the surface of the cave floor; no specimens were collected and retained.

FAMILY CHAROPIDAE. All New Caledonian endodontoids were placed by Franc (1957) and Solem (1961) in the Endodontidae. However, Solem (1976, 1983) restricted the Endodontidae to Polynesian species, with all the New Caledonian species being placed in the Charopidae. Solem et al. (1984) and Mordan and Tillier (1986) followed this family assignment. The genus *Andrefrancia* was established by Solem (1960) but may not be valid (Pawlowska 2002). However, in the absence of a more recent revision of the New Caledonian charopids, we adopt the classification of Solem (1961), acknowledging the changes in *Pararhytida* of Mordan and Tillier (1986). The fauna consisted of seven species.

Andrefrancia dispersa is distinguished by its strong, widely spaced transverse sculpture and by almost imperceptible spiral sculpture on the protoconch, visible on only some of our specimens. It was found in only two samples, NC/f1242 and f1247 (both post-European).

Andrefrancia taslei also has strong, widely spaced transverse sculpture, but its umbilicus is especially wide and deep and the shell is flat with a nonprotruding spire. It was found only in NC/f1247 (post-European).

Andrefrancia vetula was the most common charopid and one of the most common species in the overall fauna. The small shells are distinct in morphology; the transverse sculpture is finer than that of *A. rhizophorarum* (Gassies 1865), the only species with which it might be confused but which was not recorded in this study. *Andrefrancia vetula* was found in all samples except NC/f1246, f1252, and f1250 (that is, at all depths except below 72 cm).

Monomphalus bavayi is readily identified by its depressed spire, large size, and dark and mottled coloration, which remained visible on the single specimen found, in sample NC/f1249 (pre-European).

Pararhytida sp. The single, small, poorly preserved specimen, found in sample NC/f1245 (pre-European), could not be identified. Its occurrence at the cave site does not agree with the distributions of any of the six species of *Pararhytida* recognized by Mordan and Tillier (1986).

Platyrhytida saisseti is fairly easily identified, although the umbilicus of our specimens appears narrower than in the illustration of Franc (1957), suggesting that they might belong to a different, possibly undescribed species. It was found in large numbers but only in sample NC/f1249 (pre-European).

Tropidotropis trichocoma has a distinctively keeled, flat shell. Only one specimen was found, in sample NC/f1248 (pre-European).

SUPERFAMILY LIMACOIDEA, INCERTAE SEDIS. With the exception of a number of known modern introductions, the native New Caledonian limacoid snails are extremely poorly known, to the extent that Solem (1961) declined to place them in any family and was not even sure whether they are native or introduced. Franc (1957) placed the five supposedly endemic species in the Helicarionidae. Solem (1961) tentatively placed three of these five in the genus *Orpiella*, with the remaining two as "Pulmonata incertae sedis." *Orpiella* has been placed in the Helicarionidae (e.g., Vaught 1989), although Solem (1959:298) considered the Helicarionidae to be absent from New Caledonia. The helicarionid subfamily Microcystinae was shown by Solem (1959:269) as absent from New Caledonia although present to the north in Vanuatu and to the south on Norfolk Island. Possibly, these New Caledonian species are indeed helicarionids related to those of Vanuatu and elsewhere in Melanesia. Only a single species was recorded. We tentatively list it under Helicarionidae in Table 1 and tentatively identify it as a species of *Micro-*

cystis. It was recorded in all samples except NC/f1245, f1246, and f1250, suggesting that although its true identity is not certain it is indeed a native New Caledonian species.

FAMILY BULIMULIDAE. Bulimulids are represented in New Caledonia by the single genus *Placostylus*. Conchological variation in *Placostylus* has resulted in a plethora of specific names; see, for example, the synonymy under *P. fibratus* (Martyn 1789) given by Solem (1961). The range of variation within *P. salomonis* (Pfeiffer 1852) from Vanuatu, especially regarding the elongation of the shell spire, is particularly noteworthy. Two species were recorded, *P. porphyrostomus* and *P. duplex*. The specimens of *P. porphyrostomus* are in good agreement with the illustration of Franc (1957), but the specimens of *P. duplex* have a noticeably shorter spire than in his illustration. However, *P. duplex* is the closest match of all those treated by Franc (1957), and given the variation in spire elongation just mentioned for *P. salomonis*, the identification is probably correct. *Placostylus porphyrostomus* was present in samples NC/f1247 (post-European) and NC/f1248 and f1252 (pre-European). *Placostylus duplex* was found in sample NC/f1250, which is before human colonization. In addition, unidentifiable shell fragments, referable only to *Placostylus* sp. but probably belonging to one of the two mentioned species, were found in samples NC/f1244, f124, and f1245 (all pre-European).

ORDER ORTHURETHRA, INCERTAE SEDIS. Tillier and Mordan (1995) revised New Caledonian *Draparnaudia*, recognizing six species. They refuted Solem's (1962) placement of *Draparnaudia* (as the single genus in the subfamily Draparnaudiinae) in the family Enidae (which is a junior synonym of Buliminidae [Vaught 1989]). However, although they then considered *Draparnaudia* as the probable sister group to the family Partulidae, they did not raise Draparnaudiinae to family status, nor did they refer the group to another orthurethran family. There is now molecular evidence that *Draparnaudia* is the sister group to *Gastrocopta* (P. B. Mordan and C. M. Wade, unpubl. data). The single specimen, found in sample NC/f1245 (pre-European), is identified as *Draparnaudia walkeri* and is in close agreement with photographs of the lectotype (Solem 1959, Tillier and Mordan 1995).

FAMILY RHYTIDIDAE. Franc (1957) and Solem (1960, 1961, 1962, 1964) used the family name Paryphantidae, which is a junior synonym of Rhytididae (Cowie 1998). Rhytidids are sometimes difficult to distinguish from charopids on the basis of the shells alone, although the two families are not closely related. Solem (1961) changed some of the family assignments of Franc (1957); we follow Solem (1961). The fauna consisted of four species.

Specimens identified as *Rhytida aulacospira* are in close agreement with photographs of a syntype given by Solem (1959). This species was one of the most common species recorded from the cave, being found in samples NC/f1242, f1245, f1247, f1248, and f1249, which cover the entire depth range with the exception of the deepest horizon (below 72 cm).

Other specimens, similar to *R. aulacospira* but differing from it in the rate of whorl expansion and the wider spacing of the spiral sculpture (especially on the underside of the shell), cannot be identified as a described species and are referred to *Rhytida* (*Ptychorhytida*) cf. *aulacospira*. Franc's (1957) illustration of "*R. aulacospira*" resembles this species in terms of whorl expansion more than it does Solem's (1959) illustration of a syntype of *R. aulacospira*, suggesting that Franc (1957) misidentified his material. It was found in samples NC/f1242, f1243, f1247, and f1248 (0–40 cm depth).

A single specimen, probably juvenile, found in sample NC/f1247 (post-European), was identified as *Rhytida* (*Ptychorhytida*) *gassiesiana*. It matches the description given by Franc (1957) as well as his photograph of the "type." In describing this species, Preston (1907) did not designate a holotype, so Franc's (1957) figuring of the "type" probably constitutes a lectotype designation. Although Franc (1957) included it in the Charopidae, Solem (1961), followed here, considered it a rhytidid.

TABLE 2

Numbers of Specimens of *Andrefrancia vetula*, ?*Microcystis* sp., *Rhytida aulacospira*, *Rhytida* cf. *aulacospira*, and *Rhytida inaequalis* Collected from Different Depth Horizons

Species	0–5 cm	5–15 cm	15–40 cm	40–72 cm
Andrefrancia vetula	1	23	20	16
?*Microcystis* sp.	6	6	9	1
Rhytida aulacospira	18	24	3	2
Rhytida cf. *aulacospira*	5	12	1	—
Rhytida inaequalis	5	7	12	1

Rhytida (*Ptychorhytida*) *inaequalis* is a relatively large rhytidid, readily distinguished by its distinct and regular transverse shell sculpture. It was one of the more common species, found in samples NC/f1242, f1244, f1247, f1248, f1249, and f1252, which cover the entire depth range with the exception of the deepest horizon (below 72 cm). It has been reported from Vanuatu, but according to Solem (1959) probably incorrectly.

Trends in Faunal Composition

Trends in relative abundance of native species were analyzed with contingency tables. Species for which the expected value in any cell of the contingency table was <3 or for which the observed value in any cell was 0 were excluded. Because only *Placostylus duplex* occurred (three specimens only) in the 72- to 81-cm depth horizon, this horizon was excluded. Only three species occurred in sufficient numbers to permit analysis of all other depth ranges separately: *Andrefrancia vetula*, *Rhytida aulacospira*, and *R. inaequalis* (Table 2). Significant trends were detected ($G = 53.2$, $df = 6$, $P < 0.001$), with *A. vetula* declining and *R. aulacospira* increasing (*R. inaequalis* showed no clear trend and made the smallest contribution to the value of G). By combining all depth ranges >15 cm, corresponding to arrival of Europeans, more species could be included in the analysis: *Andrefrancia vetula*, ?*Microcystis* sp., *Rhytida aulacospira*, *R.* cf. *aulacospira*, *R. inaequalis* (Table 2). Again, significant trends were detected ($G = 58.7$, $df = 8$, $P < 0.001$), and again the major contributions to the value of G included a decline of *A. vetula* and an increase of *R. aulacospira*.

DISCUSSION

The native land snail fauna of New Caledonia numbers about 110–160 known species (153: Solem 1959; 135: Solem 1961; 110: Solem et al. 1984). However, many groups within the fauna have been inadequately studied and the true number has been suggested as 300–400 with many of these species locally restricted (Tillier and Clarke 1983, Solem et al. 1984). Thus, field collections are likely to include undescribed species. In addition, in many groups, intraspecific variation in shell morphology has not been adequately characterized, so that some species, currently treated as valid, will probably in the future be synonymized. This scenario of many species being undescribed but other species having been described more than once is common in diverse tropical land snail faunas (Cowie et al. 1995, Emberton 1995). In many cases, rigorous characterization of species will require study of internal anatomy and analysis of molecular characters, but for most species such studies have not been done. Of course, our samples consisted only of shells. Because of these problems, some of our material could not be definitively identified.

Two of the species recorded are well-known aliens (*Achatina fulica*, *Allopeas gracile*), introduced to Pacific islands by people. *Achatina fulica* was found only on the surface of the cave floor; it is a twentieth-century introduction. *Allopeas gracile* was found in both pre- and post-European horizons, confirming its prehistoric introduction to the islands of the Pacific (Christensen and Kirch 1981, 1986, Kirch 1993), with the caveat that mixing of stratigraphic layers to some extent may have led to it being found lower than in the absence of mixing (Carter 1990, Goodfriend and Mitterer 1993), although Grant-Mackie et al. (2004) found no evidence for such mixing in this deposit.

Only one sample, containing only *Placostylus duplex*, was obtained from a prehuman colonization stratum, so it is not strictly possible to be certain that any of the other species is native, rather than prehistorically introduced. If any of these species are indeed alien (e.g., the species referred to as "?*Microcystis* sp."), they were probably introduced from elsewhere in Melanesia or from farther west in Australasia and southern Asia. They all belong to groups that are native to this overall region, but no phylogenetic analyses have been undertaken that would permit their precise geographic origins (and hence their native or alien status in New Caledonia) to be ascertained. We interpret them all as native (Table 1), as, implicitly, previous authors have done (e.g., Franc 1957, Solem 1961). For most species, this interpretation is almost certainly correct. Three species (*Andrefranchia dispersa*, *A. taslei*, *Rhytida gassiesiana*), although only recorded from post-European strata, are very rare. This stratigraphic distribution is explained as an artifact of sampling because, as abundance decreases, occurrence of species in samples becomes more sporadic (cf. Goodfriend and Mitterer 1993). We consider them native.

In addition to the introduction of alien species (*Allopeas gracile*, *Achatina fulica*), there are some suggestions of faunal change among the native species over the last ca. 3,500 yr. *Placostylus duplex* occurs only in a prehuman sample. Possibly it was subsequently replaced by *P. porphyrostomus*, which occurs in later horizons, but the small sample sizes do not permit this to be determined, especially because unidentified fragments of *Placostylus* sp(p). occurred at shallower depths. Of the five native species for which sufficient data are available to assess changes in their abundances over time, *Andrefrancia vetula* declined and *Rhytida aulacospira* increased. There is no clear trend among the other three species analyzed statistically. *Platyrhytida saisseti* may also have declined, but its presence in only one sample (albeit in large numbers) suggests that this could be a result of chance sampling.

Whether these changes in relative abundance have anything to do with human activities, especially arrival of Europeans, or with changing habitat or climatic conditions is not certain. However, vegetational changes, especially in lowland areas (such as the cave site), have been dramatic since European colonization, with extensive replacement of native forest by alien vegetation (Gargominy et al. 1996). At the time of excavation the hill on which the cave is located was at least partly fenced off from stock intrusion and clothed in sclerophyll forest, possibly little different from what it was in prehuman times, but the surrounding area is farmed and utterly modified from what it would have been before European arrival (see Grant-Mackie et al. 2004: pl. 1). Most native New Caledonian land snails are found only in native habitats (Mordan and Tillier 1986, Tillier and Mordan 1995), so the decline of *A. vetula* and perhaps of *P. saisseti* may have resulted from the modification of native habitat. Similarly, the presence of *Pararhytida* sp. in the cave but the apparent modern absence of any species of *Pararhytida* from the region (Mordan and Tillier 1986) may also reflect habitat change. The increase of *Rhytida aulacospira* is unexplained, unless, because it is a predatory species, it is related to availability of alien snail prey (e.g., *Allopeas gracile*), but this is conjecture.

Little other information has been reported regarding the ecological preferences of New Caledonian snails. *Draparnaudia walkeri* is found only in relatively dry environments, with rainfall <2,100 mm per year (Tillier and Mordan 1995), and the rainfall ranges for the six species of *Pararhytida* have been documented (Mordan and Tillier 1986). No information is available regarding other species. Because the distributions of many native species have probably contracted as native vegetation has been replaced by aliens, current distribution records, such as those of Mordan and Tillier (1986) and Tillier and Mordan (1995), may not reflect the natural tolerance ranges and even less the natural distribution of these species. It is therefore not possible to assess changes in the fauna in the light of possible climatic change.

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